Z. Säugetierkunde **60** (1995) 150–158

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Genetic variation of Woodland caribou (*Rangifer tarandus*) in North America

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Receipt of Ms. 25. 10. 1994
Acceptance of Ms. 22. 12. 1994

Abstract

Polyacrylamide gel electrophoresis was used to examine genetic variation in nine wild populations of woodland caribou, *Rangifer tarandus*, in North America. Serum samples were typed for 19 presumptive loci, of which only one was variable. Eleven alleles were identified at the transferrin locus. Significant variation in allele frequencies and substructuring was found throughout the range, although relatively little genetic heterogeneity occurred within populations and most of the variation was contained between population. Geographic and genetic distance were significantly related. The endangered Selkirk population appears fixed for a single allele at the transferrin locus. To maintain the residual genetic variation in this population and to slow the rate of accumulation of inbreeding, we recommend the division of Anahim and Revelstoke populations into neighborhoods and a conservative strategy of transplants from these groups, without symmetrical exchange among populations in the western region.

Introduction

Previous attempts to conserve genetic diversity in wild mammals have generally relied on the species as the conservable unit. However it is becoming increasingly evident from the experience of ex situ propagation, that long term conservation of gene pools requires the preservation of populations from various geographic regions, whether or not these are formally or taxonomically recognized subspecies, evolutionary significant units, or populations (Ryder 1986). Spatial structuring of species has implications for both management practices and refuge design. Hence understanding the geographic distribution of genetic variation within and between populations is a fundamental prerequisite for conservation efforts.

The number of caribou (*Rangifer tarandus* L.) in North America declined in the 1800's and early 1900's because of increased hunting mortality and natural predation of some herds (Bergerud 1974). Today the woodland caribou is widely distributed below the tree line in Canada but has disappeared from the contiguous United States except for a small remnant population located in the southern Selkirk Mountains of northeastern Washington, northern Idaho, and an occasional occurrence in northwestern Montana. The Selkirk population has different habitat requirements and is distinct from other caribou in being larger, darker, and more heavily antlered. Although protected, the population does not appear to be increasing in size and has been stable at 25–30 animals since 1972 (Scott and Servheen 1985). In 1984 the Selkirk caribou herd, comprising 28 animals, was listed as an endangered species (Scott and Servheen 1984). A recovery plan was approved by the U. S. Fish and Wildlife Service, which has undertaken to augment the small, isolated

Selkirk population with animals from non-endangered herds of the same subspecies (U. S. Fish and Wildl. Serv. 1985).

Whereas several investigators have examined the genetics of European, semi-domestic and wild caribou herds (Brænd 1964; Røed 1985 b, c), with the exception of the Canadian Arctic islands (Røed et al. 1986), the genetic status of North American herds has not been explored. At present little is known about genetic variation in wild populations of woodland caribou that could guide in situ genetic management of endangered herds. We thus examined the genetic variation present in nine North American caribou populations separated by distances of 20 to 4 800 km in order to identify levels of genetic variation in caribou from the Selkirk area and compare this to the levels in other populations of woodland caribou, document potential inbreeding effects, and inspect the genetics of potential transplants.

Material and methods

Blood samples were obtained from 238 caribou belonging to eight populations in northwestern and east-central Canada, and a single population in the United States (Fig. 1). Samples were collected in the course of routine management practices from Brunette Island, 1980; George River, 1982; Labrador, 1980; Pic Island, 1980; Sasaginnigak Lake, 1980–81; Slate Island, 1979, 1980, 1982–1985; Selkirk 1985; Revelstoke, 1987, and Anahim, 1987. Blood samples were collected in heparinized tubes, transported as whole blood on dry ice, and stored at –80 °C until analyzed.

Vertical slab polyacrylamide gel electrophoresis (7% gel, tris-HCl pH 8.5) was used to type each animal at the following 19 presumptive loci: acid phosphatase (3.1.3.2), albumin, alcohol dehydrogenase (1.1.1.1), aldolase (4.1.2.13), catalase (1.11.1.6), esterase-1,2,3,4(4.2.1.11), α-globulin, β-globulin, glucose-6-phosphate isomerase (5.3.1.9), glutamate-oxaloacetic triaminase 1-2 (2.6.1.1), β-hemoglobin, isocitrate dehydrogenase (1.1.1.42), lactate dehydrogenase 1-2 (1.1.1.27), mannose-6-phosphate isomerase (5.3.1.8), nucleoside phosphorylase (2.4.2.1), phosphoglucomutase 1,2,3 (5.4.2.2), 6-phosphogluconic acid dehydrogenase (1.1.1.44), sorbitol dehydrogenase (1.1.1.14), and transferrin. Upper and lower tank electrode buffers were tris-HCl (pH 7.3) and tris-glycine (pH 8.8) respectively. Serum samples were diluted 1 : 1 with blucrose, electrophoresed at 5 °C, 38 mA for approximately 10 hours, and stained according to Harris and Hopkinson (1976). Transferrins were stained with Coomassie Brilliant Blue R250 general protein stain overnight, destained in 11% acetic acid, and the mobilities of transferrin bands scored relative to two known standards.

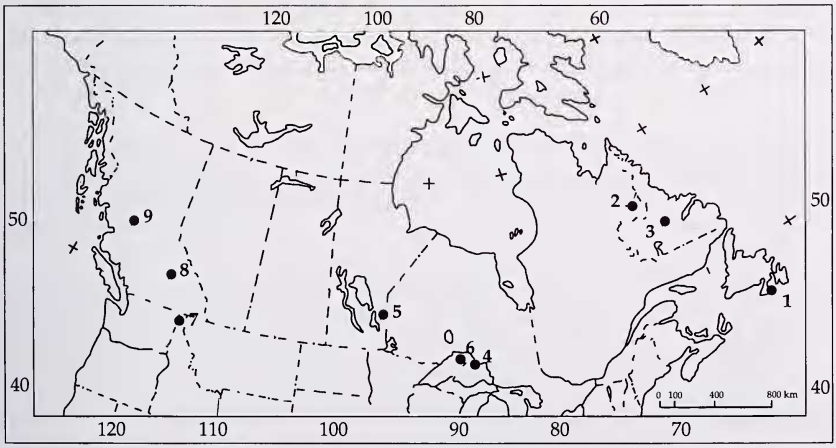

Fig. 1. Locations of nine North American *Rangifer tarandus* L. populations sampled in three regions. East: 1. Brunette Island; 2. George River; 3. Labrador, Central: 4. Pic Island; 5. Sasaginnigak Lake; 6. Slate Island, West: 7. Selkirk; 8. Revelstoke; 9. Anahim Lake.

Hierarchical analysis of population differentiation (F-statistics) was performed using the formulation of Wright (1965) as modified by Nei (1977). Chi-square contingency tables were used to determine whether populations were in Hardy-Weinberg equilibrium, and the genetic distance between each pair of populations was calculated from allelic frequency data (Rogers 1972). These data were summarized in a distance dendrogram constructed using the unweighted pair group method based on arithmetic averages (UPGMA; Sneath and Sokal 1973). The association of the matrices of genetic distance and linear, geographic distance between populations was tested using the general regression method of Mantel (1967). Changes in allele frequency of the Slate Island population over a 6-year period were analyzed by normalising the distribution (squared and arcsine transformed) and performing ANOVA using the different alleles as replicates within years.

Results

Eighteen of the loci examined were monomorphic, but the transferrin locus was highly variable with 11 alleles. Table 1 shows the allele frequencies, and heterozygosity for each population. The most common alleles were E and C for most populations. The number of alleles per population ranged from one in the Selkirk population, which appears fixed for the C allele (n = 3), to 10 in the Labrador population (n = 37; mean = 4.78). Only three of the 11 transferrin alleles were found in the British Columbia area. Woodland caribou from eastern portions of their range exhibit higher levels of polymorphism (11 alleles) and greater mean heterozygosity at the transferrin locus than do those in the west (0.50 and 0.27 respectively). All but one of the heterozygotes in the Anahim Lake and Revelstoke areas had the A_2 allele, and all of the calves (n = 5) examined from the Anahim Lake area were homozygous for the A_2 allele.

Chi square test for adherance to Hardy-Weinberg predicted frequencies (Tab. 1) indicated that the Anahim and Revelstoke populations are in Hardy-Weinberg proportions. Brunette Island, Sasaginnigak Lake, and Pic Island populations appear to conform to expectations but small sample size precludes adequate statistical testing. Slate Island ($X^2 = 36.36$, $p \leq 0.001$), Labrador ($X^2 = 12.69$, $p \leq 0.01$) and George River ($X^2 = 22.70$, $p \leq 0.001$) herds deviated significantly from Hardy-Weinberg.

Rogers' (1972) coefficients of genetic similarity (S), and distance (D), were calculated for all paired combinations of the nine populations (Tab. 2). The mean value of S was 0.5066 (range 0.125 to 0.862) and the mean D was 0.4934 (range 0.138 to 0.875). Genetic distance was greatest between the Brunette Island and Selkirk populations (0.875) and smallest between the George River and Labrador populations (0.138; Fig. 2). Predictably the Selkirk population is more similar to the Revelstoke herd (S = 0.644) than to the

Table 1. Transferrin allele frequencies (A_1–H) and heterozygosity (*H*) for nine north American *Rangifer tarandus* populations. Genotypes for three populations deviate significantly from Hardy–Weinberg, ** $0.05 < P \leq 0.01$; *** $0.01 < P \leq 0.001$. (Selkirk not tested due to small sample size). n = sample size.

Population	n	A_1	A_2	B	C	D_1	D	E_1	E	F	G	H	*H*
Brunette Island	8	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.87	0.00	0.00	0.00	0.25
George River***	46	0.04	0.15	0.24	0.03	0.00	0.20	0.02	0.28	0.04	0.00	0.00	0.74
Labrador**	37	0.03	0.08	0.15	0.03	0.05	0.30	0.00	0.19	0.08	0.05	0.04	0.51
Pic Island	4	0.00	0.13	0.25	0.25	0.00	0.00	0.00	0.37	0.00	0.00	0.00	0.75
Sasaginnigak Lake	5	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.30	0.00	0.20	1.00
Slate Island***	104	0.00	0.06	0.15	0.13	0.00	0.03	0.03	0.43	0.02	0.01	0.14	0.53
Selkirk	3	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Revelstoke	12	0.00	0.33	0.00	0.63	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.43
Anahim Lake	19	0.00	0.50	0.00	0.11	0.00	0.39	0.00	0.00	0.00	0.00	0.00	0.37

Table 2. Matrix of paired comparisons of ROGERS' (1972) genetic similarity (above diagonal) and genetic distance (below diagonal) between all pairs of nine north American populations of *Rangifer tarandus.*

Population	1	2	3	4	5	6	7	8	9
1 Brunette Island	****	0.506	0.447	0.585	0.280	0.648	0.125	0.249	0.234
2 George River	0.494	****	0.862	0.770	0.502	0.804	0.243	0.473	0.604
3 Labrador	0.553	0.138	****	0.686	0.524	0.722	0.256	0.473	0.637
4 Pic Island	0.415	0.230	0.314	****	0.547	0.834	0.375	0.559	0.490
5 Sasaginnigak Lake	0.720	0.498	0.476	0.453	****	0.535	0.564	0.641	0.412
6 Slate Island	0.352	0.196	0.278	0.166	0.465	****	0.294	0.475	0.474
7 Selkirk	0.875	0.757	0.744	0.625	0.436	0.706	****	0.644	0.223
8 Revelstoke	0.751	0.527	0.527	0.441	0.359	0.525	0.356	****	0.540
9 Anahim Lake	0.766	0.396	0.363	0.510	0.588	0.526	0.777	0.460	****

more geographically distant Anahim herd (S = 0.223) although there has been no recorded migration between these herds this century.

MANTEL matrix correlations (MANTEL 1967) indicated a significant correlation between the matrices of linear, geographic distance and ROGERS' genetic distance (P = 0.004; r = 0.551), suggesting that greater genetic divergence is associated with increased separation distance.

Hierarchical analysis of population differentiation indicates that considerable genetic heterogeneity exists among populations (Tab. 3). The total gene diversity at the transferrin locus was 36.9% with most of this attributable to between population variability. Within population variability is relatively low (9%). Regional subdivision of the total into western, central and eastern regions indictated that less than 10% of the variability is contained between regions (F_{IT} = 0.2625 and F_{IS} = 0.1811).

Microgeographic division of populations within the western region (viz. Anahim, Revelstoke, and Selkirk) indicated substantial differentiation of at least one of these populations (F_{ST} = 0.3676). Although most of the variation in this region is between populations, there is also substantial variation within populations (27%). In the central region, most of the variation is between populations (12%), but in comparison to east and particularly

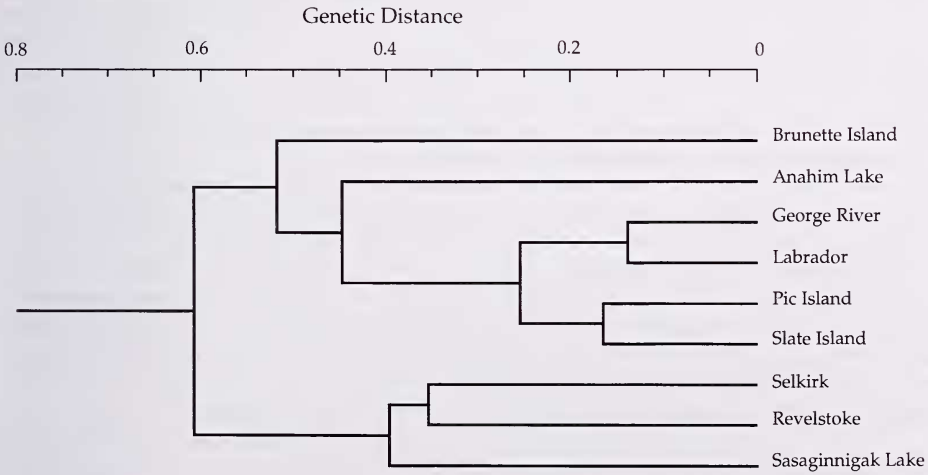

Fig. 2. Distance phenogram of nine populations of *Rangifer tarandus* clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient is 0.785.

Table 3. Hierarchical F-statistics (Wright 1978) for nine *Rangifer tarandus* populations within three regions of north America and when data for animals from all regions were combined. Significance of the F_{ST} values was determined by Chi-square and is indicated by asterisks, *** $P \leq 0.001$.

	F_{ST}	F_{IS}	F_{IT}	X^2	d.f.
Within regions					
West	.3676	.2728	.5401	249.94***	20
Central	.1245	–.0899	.0458	281.42***	20
East	.1690	.1892	.3254	307.54***	20
Between regions	.0995	.1811	.2625	473.41***	20
Total	.3070	.0906	.3698	1 461.23***	80

western regions, such differentiation is relatively low. In the east almost 17% of the variation is between the populations, with 19% within populations, and the largest proportion within individuals with respect to the region.

Although there were differences in the alleles present each year, ANOVA indicated no significant changes in allele frequencies for Slate Island over a 6-year period.

Discussion

Caribou populations in North America are characterized by low levels of genetic polymorphism but relatively high heterozygosity. Polymorphism (0.053) is less than half that of previously reported values (0.24 to 0.28; Røed 1985 b) and low even in comparison with isolated, island forms (0.11; Storset et al. 1978). However the average heterozygosity of 0.027 over 19 loci compares favorably with that for Swedish and Alaskan caribou (0.014 (n = 20) and 0.000 (n = 4) respectively; Baccus et al. 1983).

There is substantial variation at the transferrin locus in the nine populations of caribou investigated. These populations have between one and 10 transferrin alleles, with two of the island populations among the least variable. This is concordant with the findings for animal species in general (Selander 1976), as well as for other subspecies and populations of caribou. In the latter case estimates range from two to 18 (Storset et al. 1978; Røed and Whitten 1986). Maxima of 12, 13, and 18 alleles have been reported for populations in Norway, the Soviet Union, and Alaska, respectively (Shubin and Matyokov 1982; Røed 1985 a; Røed and Whitten 1986), making transferrin a potential indicator locus for monitoring genetic changes in this species.

Hierarchical F-statistics indicate that considerable genetic divergence has occurred among caribou populations within restricted geographical areas, with relatively little differentiation between the three major geographic regions. The average differentiation among populations is approximately 31% ($F_{ST} = 0.3070$; Tab. 3) which is higher than that of moose from different Scandinavian countries (9%; Ryman et al. 1980), and an order of magnitude greater than that reported for semi-domestic reindeer herds ($F_{ST} = 0.029$; Røed 1985 c). The particularly high level of differentiation noted within the western region is attributable to the fact that the Anahim population occurs on the plateau of a separate mountain range from that of the Selkirk and Revelstoke populations.

Stochastic processes such as genetic drift may play a substantial role in differentiating these populations. If migration between populations acts simply to counterbalance genetic drift then the number of caribou dispersing from different populations may be estimated by $N_em = (1/4) F_{ST} - 0.25$ (e. g., Ryman et al. 1980). For caribou in this study this implies

that less than one individual (–0.17) need migrate per generation in order to maintain the current level of genetic differentiation among all populations. The discrepancy between levels of variability in transferrin and the other loci investigated suggests that there may be significant selection on the transferrin locus, and there is some evidence that balancing selection maintains transferrin variation in caribou (RØED 1987).

Significant deviation from Hardy-Weinberg proportions was noted for Slate Island, Labrador, and George River populations. A significant WAHLUND effect (WAHLUND 1928) may be implicated for the latter populations. The George River population is large and migratory, with extensive calving grounds in Labrador, which potentially overlap the region from which the Labrador sample was derived. Additionally, the insular Slate population may be subject to strong selection pressures from maritime weather that ices vegetation (SKOOG 1968), and from extremely high population density (BERGERUD 1980).

A significant association was found between linear, geographic distance, and ROGERS' genetic distance, indicating that those populations separated the farthest geographically were also the most genetically divergent. This isolation by distance effect was apparent despite the inclusion of three insular populations. The genetic distance values for these nine populations are high compared to those reported between subspecies of caribou (0.045; RØED 1985 a), but are consistent with expectations based on direct observation of dispersal and mating patterns. Woodland caribou have a polygynous breeding structure (BANFIELD 1974), which lowers the effective population size and enhances genetic differentiation between groups. The large distance between some populations is responsible for limited gene flow among them, but genetic exchange may result in similar variation at adjacent populations (cf. George River and Labrador). In some cases, gene flow between adjacent populations occurs only under specific climatic or social conditions. For example, Pic and Slate populations, although insular, have one of the lowest genetic distance values measured, presumably because they are close enough to allow exchange of animals across the ice in winter (BERGERUD 1985). Additional opportunities for exchange of individuals occur during three periods of annual concentration, and when the paths of grazing bands cross.

There is evidence to suggest that movement restrictions on herds has profound effects on the genetic variability of wild and semi-domestic caribou herds (BRÆND 1964; RØED 1985 b), and extinction rates of insular populations (BERGERUD 1985). Such restriction would accentuate pre-existing levels of genetic differentiation and be particularly significant if, as it appears, caribou populations exhibit microspatial genetic heterogeneity. The latter is indicated by a deficiency of heterozygotes in the Svalbard caribou, and by the occurrence of different populations in different regions of the Nordenskold Land area (RØED 1985 c).

Woodland caribou from the Selkirk herd appear to be homogeneous at the transferrin locus. Possible explanations include inbreeding, a founder effect, or small and biased sampling ($n = 3$ representing 11% of the population). There are striking genetic differences between populations within the western caribou region. About 37% of the total genetic variance is explained by differences between populations. This is consistent with behavioral studies in British Columbia that indicate relatively restricted movement and philopatry of females to their calving locations (HATLER 1982, 1985). No inbreeding is indicated within the Anahim Lake or Revelstoke herds although some genotypes are not in expected proportions. Genotypes of Anahim calves suggest that either the breeders are a non-random subset of the population or a biased sample was obtained. If the sample of calves from Anahim Lake is representative then the subsequent generation may have greatly reduced genetic variation.

Extreme caution is advisable in making management recommendations based on a single variable locus, particularly one which may be under some form of selection. However the precarious situation of the small Selkirk population justifies some generalisations

regarding the probable short and long term outcomes of genetic management of the region. Much will depend on the strength of the caribou social system. According to Calef (1981), there is a high degree of plasticity in the behavior of caribou within subspecies, such that populations vary in behavior and appearance depending on their habitat and degree of isolation from other populations. If polygynous breeding is common in woodland caribou then genetic variation within herds will be lost more rapidly, whereas genetic divergence among herds will accrue more rapidly than predicted.

If indeed the low rate of population increase indicates that inbreeding has accumulated in the Selkirk population, then the first goal is to alleviate this as quickly as possible. The apparent polygynous breeding structure and relatively large harem size of the woodland caribou would enable such a reduction to occur rapidly. In the short term, transplants from Anahim and Revelstoke should reduce inbreeding and retain alleles of the Selkirk herd, thus preserving what little variation exists.

Exchange of individuals among a limited number of small populations such as in the western region may not be adequate to maintain genetic variation in the long term. While it may slow the accumulation of inbreeding, it does not alleviate the probable loss of fitness indefinitely. A higher coefficient of relationship would result among all individuals of all populations and inbreeding would increase along with a loss of alleles. The rate of accumulation of inbreeding may be slowed by avoiding symmetrical exchange amongst populations and by dividing the populations into neighborhoods with a rate of exchange between them (Chesser 1983). Similarly, if a species regularly undergoes cycles of inbreeding and outbreeding, a high degree of relatedness among individuals within breeding units will minimize loss of genetic variability overall, as units will be fixed for different alleles. Were genetic management paramount, this might be achieved by avoiding, or intermittently adopting, ungulate predator management to create population fluctuations and cycles of greater or lesser inbreeding in the western region.

The success of such in situ management of confined populations is difficult to predict in small, natural populations where stochastic processes predominate. Observation of natural movements (Ferguson 1982; Bergerud and Elliot 1986) and introductions to the Svalbard population (Røed 1985 c) have demonstrated that ecological and behavioral isolation may limit the potential contribution of transplanted animals. However given the increasing environmental pressures on the Selkirk population and the paucity of information regarding fitness determination in large mammals, conservation of the current level of genetic variation is prudent.

Acknowledgements

We thank G. Servheen for providing blood samples, and R. Huber for translating the German summary and commenting on previous versions of the manuscript. This work was supported by the University of Natal (Durban), the Foundation for Research Development, the Graduate School at Texas Tech University (MvS), and the U.S. Fish and Wildlife Service (RKC).

Zusammenfassung

Genetische Variabilität beim Karibu (Rangifer tarandus) in Nordamerika

Die genetische Variabilität von neun nordamerikanischen Populationen des Waldkaribu (*Rangifer tarandus*) wurde mittels Polyacrylamidgel-Elektrophorese untersucht. Serumproben wurden auf genetische Variation an 19 auswertbaren hypothetischen Genloci geprüft, wobei sich am Transferrinlocus ein Polymorphismus für 11 Allele nachweisen ließ. Es zeigten sich signifikante Unterschiede in den Allelhäufigkeiten und ein hoher Anteil der genetischen Variabilität entfiel auf die genetische Differenzie-

rung zwischen den Populationen. Die genetischen Distanzen waren mit den geographischen Abständen signifikant korreliert. In der bedrohten Population von Selkirk scheint am Transferrinlocus ein Allel fixiert zu sein. Um die noch verbliebene genetische Variabilität in diesem Bestand zu erhalten und den Anstieg des Inzuchtgrades zu verringern, empfehlen wir die Aufteilung der Populationen von Anahim und Revelstoke in „Nachbarschaften". Eine kontrollierte Einbringung von Individuen dieser Gruppen nach Selkirk ohne symmetrischen Austausch zwischen den Populationen der westlichen Region erscheint angezeigt.

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